Vocal evidence for species rank to *Cercomacra nigrescens fuscicauda* J. T. Zimmer

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SUMMARY.—Vocal analysis confirms that male song of the west Amazonian form of Blackish Antbird *Cercomacra nigrescens fuscicauda* differs distinctly from songs of other forms of the species including in areas where their ranges meet, an indication that *fuscicauda* is reproductively isolated from adjacent taxa. Elevating *fuscicauda* to species rank leaves *C. nigrescens* with disjunct but vocally fairly similar populations.

The genus *Cercomacra* P. L. Sclater, 1858, encompasses 25 cryptic taxa presently ranked as 12 species, all medium-sized, fairly long-tailed, often with fairly horizontal posture, and all vocally distinct. Three of the species were only recognised recently (Fitzpatrick & Willard 1990, Bierregaard *et al.* 1997, Graves 1997). The genus has been divided into two major species groups: *C.* [*tyrannina*] and *C.* [*nigricans*] each including five species. The remaining two species (Rio de Janeiro *C. brasiliana* and Grey Antbirds *C. cinerascens*) are of uncertain relationships but may be intermediate between the two groups (Zimmer & Isler 2003).

The *C.* [*tyrannina*] group includes Blackish *C. nigrescens*, Willis's *C. laeta*, Dusky *C. tyrannina*, Parker's *C. parkeri* and Black Antbirds *C. serva*. They occur in secondary undergrowth and river and lake edge habitats from southern Mexico to the Guianas, central Brazil, and northern Bolivia (Zimmer & Isler 2003). The geographical ranges of its component species are largely allo- or parapatric, and where they meet or overlap slightly, the species usually differ in habitat (Zimmer & Isler 2003). The only exception is the range of *C. serva*. It covers almost the entire range of *C. nigrescens fuscicauda* and overlaps slightly with the Andean forms of *C. nigrescens*.

Zimmer (1931) described three new taxa of *Cercomacra* from eastern Ecuador, eastern Peru and northern Bolivia, *aequatorialis* and *notata* from the foothills of the Andes, intergrading in San Martín, Peru, and *fuscicauda* from the adjacent Amazonian lowlands. Despite the distinctive female plumage of *fuscicauda* and its close geographical proximity to the Andean forms, he ranked all three as subspecies of *C. nigrescens* (Cabanis & Heine, 1859), a species otherwise known from populations in the Guianas (*nigrescens*) and central Brazil (*approximans, ochrogyna*).

The type locality of *fuscicauda* is Lagarto, on the río Ucayali near the mouth of the Urubamba, Peru (Zimmer 1931). Birds tape-recorded along the river nearby (MLNS 165676; for acronym see Methods) vocalise similarly to lowland birds from throughout eastern Ecuador, eastern Peru and western Brazil. Additionally, a dependent immature male was collected (Academy of Natural Sciences Philadelphia 177794) after its loudsong, similar to that of an adult male, was tape-recorded (MLNS 37541) in Loreto, Peru, establishing that the name *fuscicauda* is correctly assigned to this vocal type.

Males of all six forms of *C. nigrescens* are rather similar, grey above, slightly paler below, with narrow white tips to the wing-coverts, small white shoulder patch and semi-concealed white interscapular patch. Nominate *nigrescens* is darkest, the central Brazilian and Andean taxa palest, while west Amazonian *fuscicauda* is nearly as dark as the nominate, relatively dark below, and usually has a faint 'bluish' bloom (Zimmer 1931). The white interscapular and shoulder patches in *fuscicauda* average smaller than in other forms, and the white tips

to the wing-coverts narrower than in the Andean and central Brazilian taxa, but males of all forms are rather variable. Nominate *nigrescens* often lacks white tips to the wing-coverts altogether (Cory & Hellmayr 1924), one male specimen of *fuscicauda* from La Paz, Bolivia, was considered intermediate in plumage between *fuscicauda* and *approximans*, and some *fuscicauda* are noticeably large-billed (Zimmer 1931), rendering it difficult to identify male specimens to subspecies with certainty.

Females, in contrast, are more easily identified to subspecies group. They have greyish-brown upperparts and flanks, ochraceous forehead, lores, superciliary region and most of the underparts, and faintly indicated pale tips or fringes to the wing-coverts (Cory & Hellmayr 1924, Zimmer 1931). The tail is fuscous in the Guianas and Brazil, pale brown in the Andes, blackish fringed olivaceous in *fuscicauda*. Female *fuscicauda* is paler and duller ochraceous than the rest, and has the crown washed tawny, thus showing a markedly less contrasting facial pattern; additionally, its flanks are greyer and wing-coverts more clearly marked with light Dresden Brown (as of Ridgway 1912) than the other forms (Zimmer 1931, Schulenberg *et al.* 2007).

The voices of these taxa were unknown when Zimmer (1931) and Hellmayr (Cory & Hellmayr 1924) wrote. During the 1980s T. A. Parker recorded the voices of all forms of *C. nigrescens* except the nominate (MLNS recordings), but he never published on the different voice of *fuscicauda*. Mayer (1996) presented recordings of *fuscicauda* and *approximans* from north-east Bolivia and suggested that they were not conspecific. Around the same time (early 1990s), P. Coopmans discovered that two vocal types occurred in different habitats and elevations in Ecuador (Ridgely & Greenfield 2001). The distinctive voice of *fuscicauda* was also noted by Zimmer & Isler (2003) and Schulenberg *et al.* (2007), but a comparative analysis was never published.

We present the results of such an analysis and demonstrate that male song of *fuscicauda* differs markedly from the other five subspecies in two vocal characters, with non-overlapping distributions of data for number of notes and pace. According to Isler *et al.* (1998) a member of Thamnophilidae is unlikely to interbreed with other forms if its song differs consistently in at least three characters, but for parapatric taxa fewer than three diagnosable characters can be considered appropriate. With significant difference in two characters, we add the lack of intermediate song types in areas of parapatry as evidence that *fuscicauda* does not interbreed with geographically adjacent forms, and conclude that it should be ranked as a biological species.

Methods

Vocal material obtained during field studies, from published recordings (Isler & Whitney 2002, Krabbe & Nilsson 2003, Lysinger *et al.* 2005, Moore *et al.* 2009), and from the public archives Macaulay Library of Natural Sounds (MLNS) and XenoCanto (XC) were compared using the sound-editing programme CoolEditPro (Syntrillium Software). Recordings of all six subspecies were analysed. The major types of vocalisations and number of recordings examined are specified in Table 1.

We compared 161 recordings of male song, from the majority of known localities: *nigrescens* from French Guiana, Surinam, Guyana, Roraima and northern Amazonas, Brazil, north of the Amazon River; *approximans* from Santa Cruz, Bolivia, Amazonas, Rondônia, Mato Grosso and Pará, Brazil; *ochrogyna* from Pará, Brazil; *aequatorialis* from Napo, Morona-Santiago and Zamora-Chinchipe, Ecuador; possible *aequatorialis* / *notata* intergrades from San Martín and Amazonas, Peru; *notata* from Huánuco, Loreto, Pasco, Ucayali, Junín and Cuzco, Peru. Recordings of *fuscicauda* were obtained from Amazonas, Colombia; Sucumbíos, Orellana, Napo and Pastaza, Ecuador; Loreto, Ucayali, Madre de Dios and Cuzco, Peru;

TABLE 1

Major types of vocalisations and number of recordings examined for each of the six subspecies of Blackish Antbird *Cercomacra nigrescens*.

Taxon	aequatorialis	aequatorialis/ notata	notata	approximans	ochrogyna	nigrescens	fuscicauda
Male song	20	9	23	39	8	14	46
Female song	15	2	13	21	6	12	25
Contact call	3	0	4	15	2	9	27
Churred calls	8	0	3	17	3	9	11
Other calls	0	0	0	0	0	0	10

Acre and south-west Amazonas, Brazil; and Beni, Bolivia. The only region of interest from which no tape-recordings were examined is the upper Mamoré drainage in Cochabamba, Bolivia, which is the only part of the range of *fuscicauda* where *C. serva* is absent. All songs comprised an introductory note followed by a rattle. They were measured for total duration and duration of the introductory note, and the rattle was measured for number of notes, duration, mean pace, pace at start and end, and pitch of highest and lowest note.

We compared 94 recordings of female song from most of the same localities. Female songs, comprised of a rising series of notes, were measured for number of notes, duration, and pitch of first and last note. Additionally, we compared 121 recordings of various calls.

Diagnostic differences had to be discrete, non-overlapping character states that have the potential for unambiguous signal recognition (Isler *et al*. 1998). Ranges of samples of continuous variables could not overlap, and the likelihood that ranges would not overlap with larger sample sizes was estimated by tests described in detail in earlier publications (e.g., Isler & Whitney 2011).

Results

Duets of *Cercomacra nigrescens* typically comprised three songs, male-female-male, and the female song usually partly overlapped in time with one or both male songs, and the second male song was often longer, with more notes than the first.

Male song in all forms of *C. nigrescens* was composed of a low-pitched introductory note followed by a rattle of descending notes (Fig. 1). In *fuscicauda* the rattle differed drastically from all other forms in being composed of a much larger number of notes given at a much faster pace. In all other forms there was considerable overlap in pace and number of notes. In *fuscicauda* the pitch usually rose slightly (1.8 ± 1.1 half notes on a chromatic scale, range 0.0–4.2) at the beginning of the rattle (only remaining constant in one of 42 recordings), and always dropped markedly towards the end, whereas in the other forms the pitch descended evenly or occasionally remained constant. On average, *fuscicauda* songs also differed, albeit with overlap, in a longer introductory note, higher max. pitch of the rattle and in decelerating rather than accelerating pace (Table 2). Eight recordings from the tributaries of the Xingu and Tocantins rivers were tentatively referred to *ochrogyna*. While the rattle of male song recorded near the mouth of the rio Xingu resembles *approximans* in all respects, the rattles in recordings from 480 km to the south (middle rio Xingu) and 350 km south-east (upper rio Itacayunas, a tributary of the rio Tocantins) all showed fairly constant pitch and decidedly slower pace (Fig. 2).

The number of notes and mean pace of male loudsongs of *fuscicauda* differed measurably from those of all other populations (Table 2). The ranges of these measurements
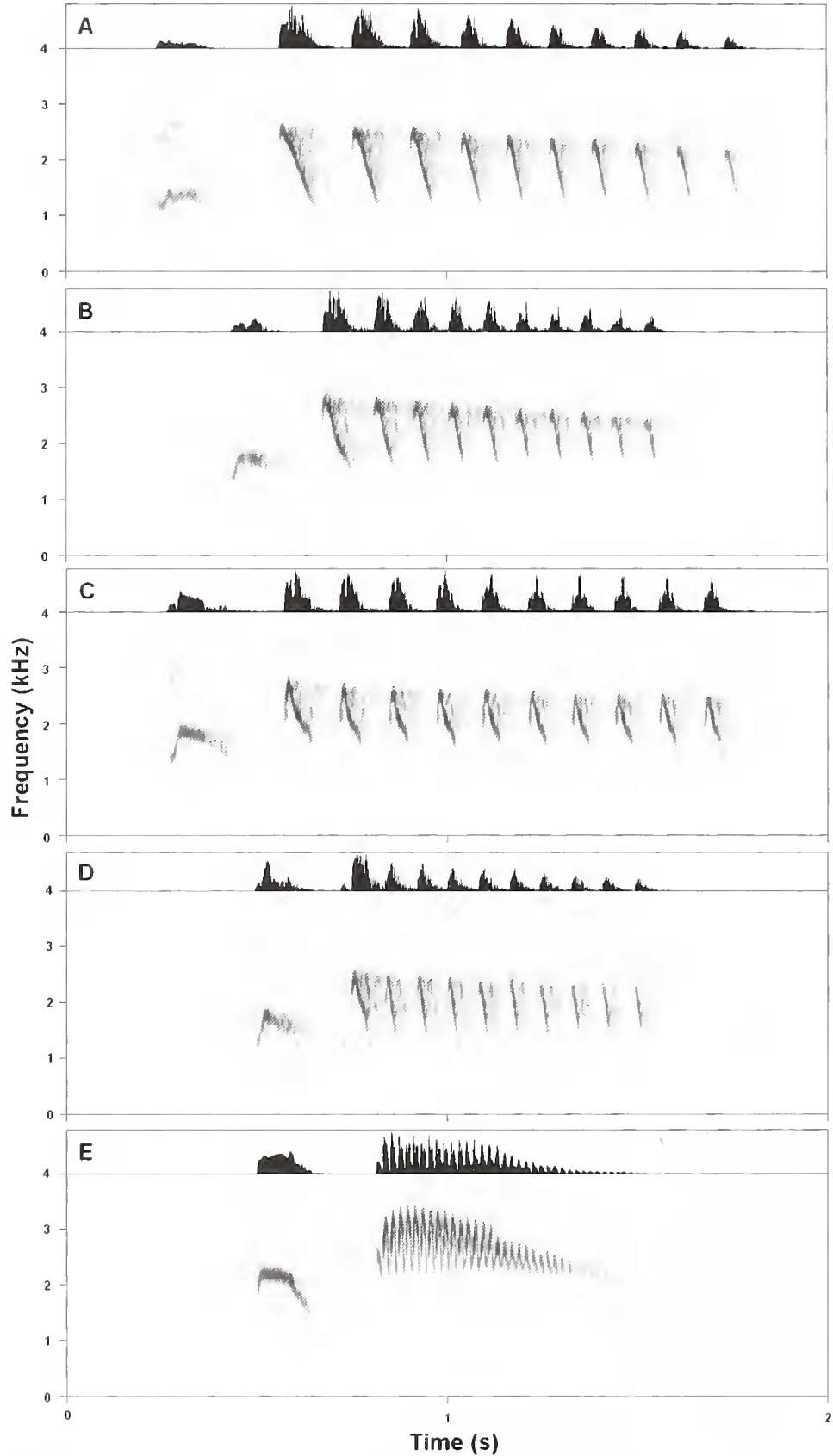
Figure 1. Oscillograms and sonograms of male songs of different taxa referred to Blackish Antbird *Cercomacra nigrescens*. A: *C. n. aequatorialis*; B: *C. n. notata*; C: *C. n. approximans*; D: *C. n. nigrescens*; E: *C. n. fuscicauda*. Note the drastically different song of *fuscicauda*.

TABLE 2

Some properties of male song of different taxa of Blackish Antbird *Cercomacra nigrescens* (mean ± standard deviation, range, sample size). First six rows measure the rattle alone. Change in pitch is measured in half notes on a chromatic scale ((ln(pitch of highest note/pitch of last note))/ln$^{12}\sqrt{2}$), change in pace from start of second to start of third, and start of penultimate to start of last note. Note the drastically fast pace in *fuscicauda*, and the slow pace and lack of change in pitch in *ochrogyna*.

Taxon	*aequatorialis*	*notata*	*approximans*	*ochrogyna*	*nigrescens*	*fuscicauda*
No. notes	9 ± 2 (7–13) n = 20	12 ± 3 (10–21) n = 23	9 ± 2 (7–15) n = 39	8 ± 2 (6–11) n = 8	13 ± 4 (8–21) n = 14	32 ± 6 (23–48) n = 38
Duration (seconds)	1.1 ± 0.3 (0.7–1.5) n = 20	1.1 ± 0.2 (0.7–1.6) n = 23	0.9 ± 0.3 (0.5–1.5) n = 39	1.5 ± 0.3 (1.1–2.0) n = 8	1.1 ± 0.4 (0.6–1.7) n = 14	0.6 ± 0.1 (0.4–0.8) n = 46
Mean pace (notes / seconds)	8 ± 1 (6–9) n = 20	11 ± 1 (9–14) n = 23	10 ± 2 (6–14) n = 39	5 ± 1 (3–8) n = 8	12 ± 1 (10–13) n = 14	53 ± 5 (44–62) n = 38
Δ pace	1.32 ± 0.14 (1.15–1.65) n = 20	1.16 ± 0.20 (0.91–1.72) n = 23	1.09 ± 0.17 (0.89–1.95) n = 39	1.19 ± 0.12 (1.03–1.41) n = 8	1.09 ± 0.22 (0.86–1.75) n =14	0.90 ± 0.14 (0.62–1.13) n = 38
Highest pitch (Hz)	2,641 ± 114 (2,482–2,873) n = 20	2,598 ± 124 (2,231–2,832) n = 23	2,728 ± 225 (2,428–3,292) n = 38	2,538 ± 132 (2,313–2,616) n = 8	2,275 ± 144 (2,048–2,525) n = 14	2,880 ± 209 (2,520–3,377) n = 42
Δ pitch (half notes)	2.4 ± 0.8 (0.8–3.9) n = 20	3.4 ± 0.7 (2.5–4.9) n = 23	2.4 ± 1.1 (0.4–4.7) n = 38	0.4 ± 0.4 (0.0–1.1) n = 8	2.0 ± 0.9 (0.3–3.4) n = 14	6.5 ± 2.9 (0.6–12.4) n = 42
Duration of introductory note (seconds)	0.15 ± 0.02 (0.11–0.18) n = 20	0.12 ± 0.02 (0.10–0.17) n =23	0.14 ± 0.02 (0.09–0.20) n = 39	0.15 ± 0.02 (0.12–0.18) n = 8	0.12 ± 0.02 (0.10–0.17) n = 14	0.17 ± 0.03 (0.13–0.28) n = 46

TABLE 3

Some properties of female songs of different taxa of Blackish Antbird *Cercomacra nigrescens* (mean ± standard deviation, range, sample size). Note the similarity.

Taxon	*aequatorialis*	*notata*	*approximans*	*ochrogyna*	*nigrescens*	*fuscicauda*
No. notes	6 ± 1 (5–8) n = 15	7 ± 1 (6–10) n = 13	6 ± 1 (5–11) n = 21	7 ± 1 (6–8) n = 6	6 ± 1 (4–9) n = 12	5 ± 1 (3–7) n = 25
Duration (seconds)	1.9 ± 0.4 (1.4–2.6) n = 15	2.3 ± 0.4 (1.8–3.1) n = 18	1.9 ± 0.4 (1.4–2.9) n = 21	2.2 ± 0.3 (1.7–2.5) n = 6	1.9 ± 0.4 (1.2–2.5) n = 12	1.7 ± 0.3 (0.9–2.1) n = 25
Pitch of first note (Hz)	1,572 ± 203 (1,280–2,019) n = 15	1,351 ± 116 (1,172–1,473) n = 13	1,578 ± 157 (1,320–1,830) n = 21	1,578 ± 118 (1,375–1,676) n = 6	1,397 ± 150 (1,236–1,777) n = 12	1,624 ± 223 (1,331–2,189) n = 25
Pitch of last note (Hz)	2,503 ± 216 (2,062–2,842) n = 15	2,285 ± 252 (1,729–2,547) n = 13	2,336 ± 248 (1,824–2,706) n = 21	2,260 ± 308 (1,957–2,829) n = 6	2,146 ± 187 (1,934–2,445) n = 12	2,539 ± 342 (1,783–3,054) n = 25

did not overlap and distributions met tests of the likelihood that they would not overlap with larger samples. Therefore, the two independent measures are considered diagnostic.

No intermediate song types between *fuscicauda* and adjacent forms were found. Recordings from Napo, Ecuador, where *aequatorialis* and *fuscicauda* were found just 30 km apart, recordings from Ucayali, Peru, where *notata* was found only 12 km from the río Ucayali near the type locality of *fuscicauda*, and recordings from Beni, Bolivia, where *approximans* and
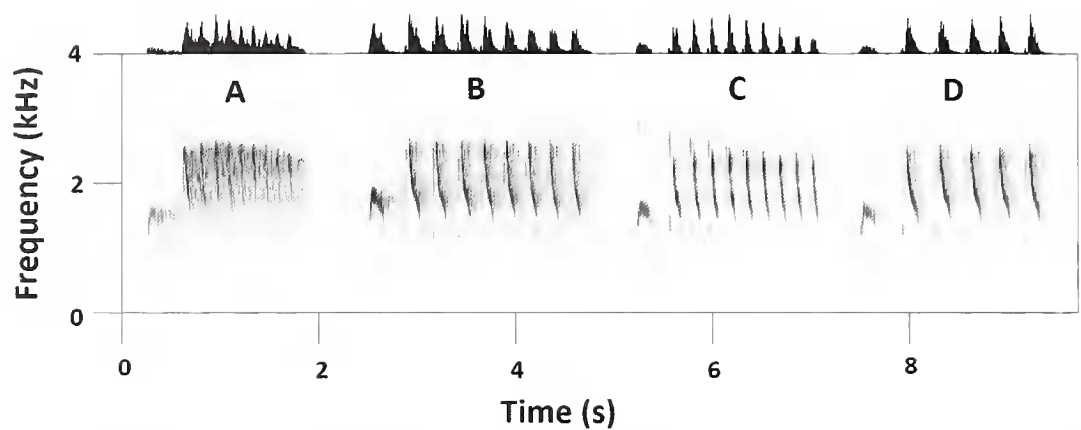
Figure 2. Oscillograms and sonograms of male song in recordings tentatively referred to *Cercomacra nigrescens ochrogyna* from east Amazonian Brazil. A: near mouth of rio Xingu; B: middle rio Xingu; C–D: Serra dos Carajás (rio Tocantins drainage). While the song in A resembles that of *approximans*, songs in B, C and D are slower paced and average more constant in pitch.
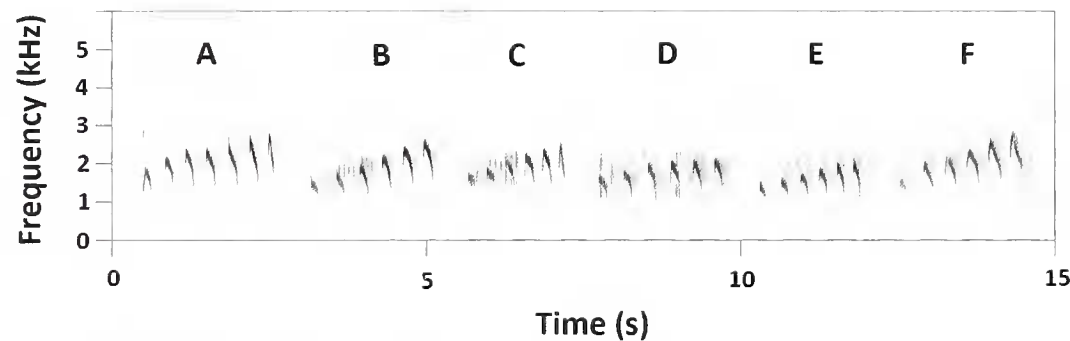

Figure 3. Sonogram of female songs of different taxa referred to Blackish Antbird *Cercomacra nigrescens*. A: *C. n. aequatorialis*; B: *C. n. notata*; C: *C. n. approximans*; D: *C. n. ochrogyna*; E: *C. n. nigrescens*; F: *C. n. fuscicauda*. Note the similarity.
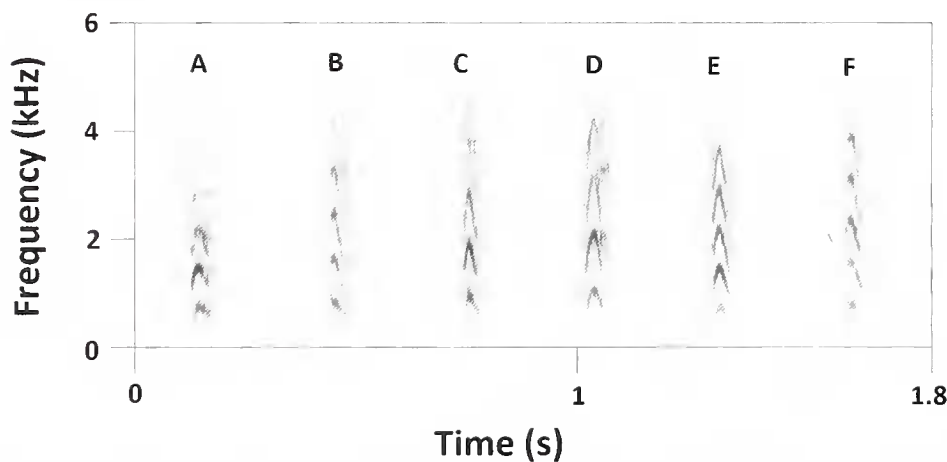

Figure 4. Sonogram of contact call of different taxa referred to Blackish Antbird *Cercomacra nigrescens*. A: *C. n. aequatorialis*; B: *C. n. notata*; C: *C. n. approximans*; D: *C. n. ochrogyna*; E: *C. n. nigrescens*; F: *C. n. fuscicauda*. Note the similarity.

fuscicauda occurred just 80 km from each other, were all clearly of one song type or the other. We detected no obvious habitat barrier between them in any of these areas.

Female song in all six forms was a series of 3–11 notes rising steadily from *c*.1,500 Hz to *c*.2,350 Hz and given at a fairly steady pace of *c*.3 notes per second. At the onset of duets
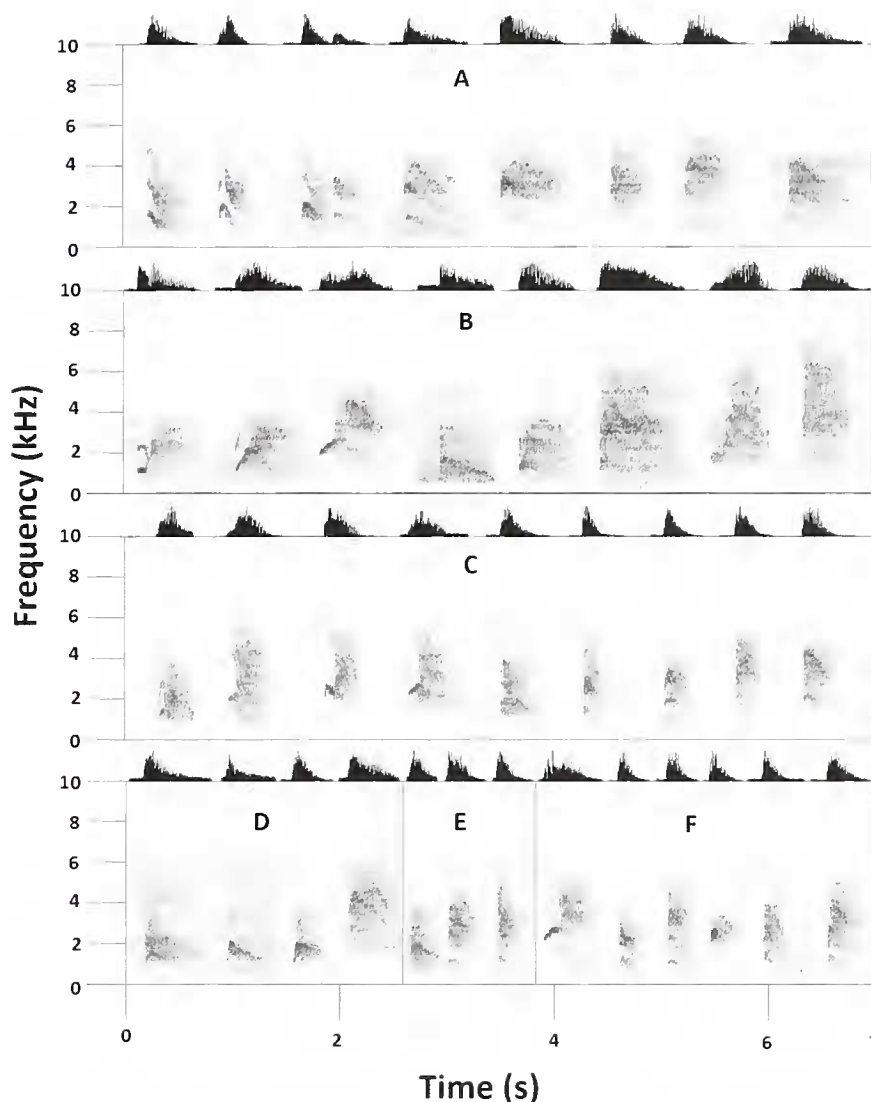
Figure 5. Oscillograms and sonograms of churred calls of Blackish Antbird *Cercomacra nigrescens*. A: *C. n. fuscicauda*; B: *C. n. aequatorialis*; C: *C. n. approximans*; D: *C. n. notata*; E: *C. n. ochrogyna*; F: *C. n. nigrescens*. Note that calls of *approximans*, *ochrogyna* and *nigrescens* average shorter than the others, but the general range of variation was so great that homology was difficult to verify.

it comprised fewer notes than later in the bout. As also found by Zimmer & Isler (2003) it was very similar in all six forms (Fig. 3). The last note was sometimes of slightly different quality, and at least in *aequatorialis, notata, approximans, ochrogyna* and *fuscicauda* the song was very rarely terminated with a few rapid notes, higher or lower, sometimes reminiscent of the male rattle. Female song (both beginning and end) averaged slightly higher pitched in *fuscicauda* than in other forms (Table 3).

Call notes recorded were of a variety of types. The most commonly recorded call was a single, slightly nasal note given by both sexes, apparently in contact. All six forms gave very similar versions of this call (Fig. 4).

Churred disturbance calls were slightly higher pitched in females than in males. They were given at various levels of excitement and differed widely in structure and quality, even within a single form (Fig. 5), rendering an assessment of homology difficult. However, most of the churred calls given by *approximans, ochrogyna* and *nigrescens* were shorter than those given by other forms (Fig. 5).
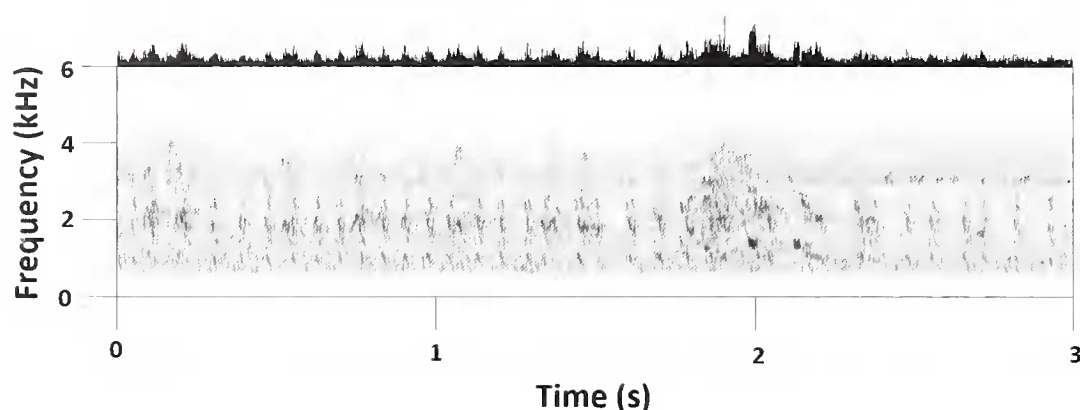
Figure 6. Oscillogram and sonogram of calls of a pair of *Cercomacra nigrescens fuscicauda* during a territorial dispute. This call of rapidly repeated notes weak in overtones compared to the contact call in Fig. 4 was sometimes sustained for 15 seconds or more, both members of the pair giving synchronised, higher pitched, louder bursts at intervals, in this example at start and after *c*.2 seconds.
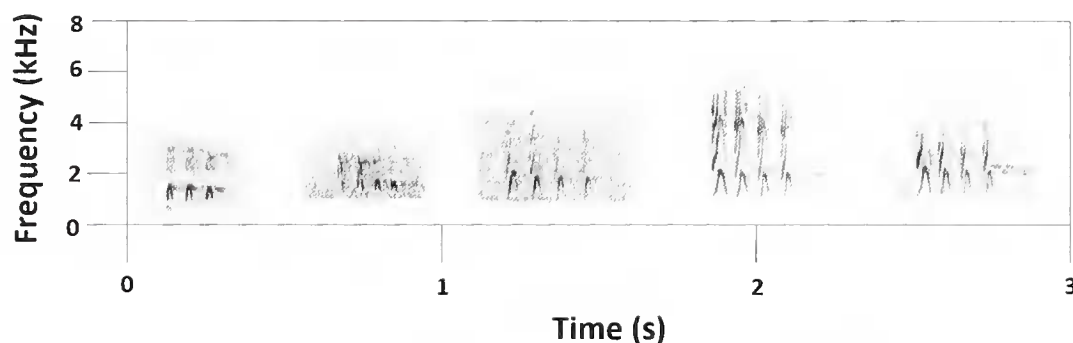

Figure 7. Sonogram of calls by five individuals of *Cercomacra nigrescens fuscicauda*. This rapid series of 3–4 notes was given by agitated birds and might be unique to *fuscicauda*.

Ten recordings of *fuscicauda* included other call types given during territorial disputes. Four of them were of a pair giving a longer series of low-pitched notes with weaker overtones than the contact calls, mainly at constant pitch, but interspersed at intervals by bursts of higher pitched louder notes (Fig. 6). Such bursts sometimes terminated longer series with a call of three or four notes in rapid succession, a call also given alone in high excitement or in alarm by surprised fleeing birds (Fig. 7).

Discussion

Habitat and geographic distribution.—As mentioned earlier, nearly all species in the [*C. tyrannina*] group are allo- or parapatric, and differ in habitat where their ranges overlap. Where *C. nigrescens* co-occurs with *C. tyrannina* it is mostly confined to *várzea*, *C. tyrannina* to *terra firme*, and where it co-occurs with *C. laeta* the latter is mostly confined to white-sand forest (Snethlage 1913, Zimmer 1931, Zimmer & Isler 2003). The range of *C. serva*, however, is entirely encompassed by that of *C. nigrescens*. In view of their seemingly similar habitat requirements, it is difficult to explain how they manage to co-exist in some areas. To the east, *C. serva* is replaced by *C. n. approximans* with little or no overlap, and through most of the lowland part of the range of *C. serva*, *C. n. fuscicauda* is confined to a narrow niche of seasonally flooded forest, thickets and *Gynerium* cane on river islands and banks (Ridgely & Greenfield 2001, Zimmer & Isler 2003, Schulenberg *et al.* 2007; also descriptions given for

recording sites on MLNS and XC recordings, and pers. obs.). In the south-east Peruvian lowlands and at lower elevations in the Andean foothills, however, a partitioning of niches appears to be incomplete. The Andean forms of *C. nigrescens* occur at higher elevations (to 2,100 m) than *C. serva*, but where the ranges of the two species overlap, at elevations of 700–1,100 (locally to 1,500) m, no habitat difference is apparent (Ridgely & Greenfield 2001, Schulenberg *et al.* 2007; pers. obs.). Both species can be heard on some tape-recordings, but it is possible that individual territories do not overlap. The incomplete niche partitioning in some areas and the rather local occurrence of *C. n. fuscicauda*, at least in Peru (Schulenberg *et al.* 2007) might suggest that *C. serva* expanded its range fairly recently.

Based on vocal evidence and published specimens the six described forms of *C. nigrescens* are distributed as follows.

C. n. nigrescens: Guianas. Birds from Sao João de Baliza and along the rio Branco and immediately adjacent rio Negro, Roraima, Brazil (Naka *et al.* 2007) are vocally similar and are tentatively referred here. A recording from the mouth of the rio Japurá nearly 600 km west of Manaus (M. Cohn-Haft, unpubl.) probably also belongs here. 0–90 m.

C. n. approximans and *ochrogyna*: from rio Madeira, western Amazonas, Brazil, and Beni and Santa Cruz, north-east Bolivia east through Rondônia and Mato Grosso to Pará, Brazil, generally south of the Amazon, but locally on both banks. The range of *ochrogyna* is uncertain. The type locality is on the rio Araguaia (an affluent of the rio Tocantins) in extreme north-east Mato Grosso, and no recordings are available from there or the immediate vicinity. We tentatively refer all birds from the Xingu and Tocantins drainages to this form, but note that song recorded near the mouth of the rio Xingu resembles that of *approximans*, while songs from near the middle rio Xingu (Pinkaiti on the rio Riozinho) and the Tocantins drainage (Serra dos Carajás) are slower paced and possibly more constant in pitch (Fig. 2). 10–660 m.

C. n. aequatorialis and *notata*: from northern Napo, eastern Ecuador (*aequatorialis*) south to north-west Cusco, south-east Peru (*notata*), intergrading in San Martín, Peru. 700–2,100 m.

C. n. fuscicauda: from Napo and Sucumbíos, Ecuador, and south-east Amazonas, Colombia (Leticia) south through eastern Peru and adjacent Acre and south Amazonas (upper rio Purus drainage: unpubl. recordings by M. Cohn-Haft), Brazil, to northern Beni and Cochabamba, Bolivia. 100–600 m, locally to 850 m (XC57243). In Beni recorded only 80 km from *approximans*, in Napo, just 30 km from *aequatorialis* and in Ucayali only 12 km from *notata*.

With no obvious habitat barrier between *fuscicauda* and neighbouring forms of *C. nigrescens* where they are in closest proximity, they must be presumed to come into contact with each other. The lack of intermediate song types near the contact zones is evidence that they either maintain their integrity despite limited hybridisation, or that they do not interbreed at all.

Evolution.—Without data on the genetic distances between the various forms of *C. nigrescens*, scenarios linking speciation events to the upheaval of the Andes and Amazonian dynamics caused by climatic fluctuations would be speculative. However, the similarities between female songs and contact calls do suggest that all six taxa form a monophyletic unit. Additionally, the incomplete niche partitioning with *C. serva* suggests that *fuscicauda* may have speciated as a result of a recent expansion of that species.

Elevating *fuscicauda* to species rank leaves a disjunct and possibly paraphyletic *C. nigrescens* with populations in the Guianas and Brazil north of the Amazon, in east Amazonian Brazil, and in the Andes. The Amazonian Brazil population is separated from the Andean by 850 km and from the Guianan by 350 km. These three populations may have reached genetic incompatibility and thus require consideration as species, but we

did not find vocal evidence to support this during the present study, except for possibly in *ochrogyna* (see above).

Conclusion

We suggest that *fuscicauda* be raised to the rank of biological species based on the criteria of Isler *et al.* (1998). Two vocal characters were found to differ diagnostically and the lack of recordings of intermediate song types provides evidence that *fuscicauda* does not interbreed with adjacent, clearly parapatric forms. We follow previous suggestions of Riparian Antbird (Krabbe & Nilsson 2003) as a vernacular name. Throughout much of its range *fuscicauda* is confined to seasonally flooded forest or stands of *Gynerium* cane and adjacent thickets on sandbars and river banks, and it appears to be always associated with riparian habitats, whereas the other forms of *C. nigrescens* also occur in other habitats, the Andean forms exclusively so.

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